XX.—*On the Development of the Annelides.* By M. Sars *.

[With a Plate.]

Till recently, all that was known respecting the development of the Annelides was based solely upon observations made on the leech; the other Annelides were judged of from this, and their development considered to be extremely simple, *i. e.* that the animals left the egg as perfectly formed as they appear during their whole life. To what very erroneous conclusions we frequently come in this way, and how cautious we ought to be in generalizing, abundant instances prove. So, for instance, not to mention others, it was concluded, from the knowledge of the development of the craw-fish, that all the other Decapods were in this respect similar; and naturalists were thus led to doubt for a long time, to the injury of science, the beautiful discoveries of Thompson.

In the month of February 1840 I discovered, in the examination of a *Polynoë cirrata*, Fab., that the young when they leave the egg have a very different form from that of the adult animal, and that they are deficient in most of the external organs which are so characteristic of these animals; in a word, therefore, that this Annelide is subject to a metamorphosis. I only succeeded in observing the first stage of development, and therefore kept back my observations on this subject, with numerous other imperfect notices, with the hope of being able to complete them in the course of time. However, although I had occasion to repeat the observation in February and March 1841, I could not succeed in tracing the development any further; and it might, perhaps, appear superfluous to publish these observations at present, after Lovèn has communicated to the public his far more complete observations on the metamorphoses in a species of Annelides. I do it however partly to confirm the latter, which no one yet has done, and partly because I am able, which was not the case with Lovèn, to point out a known species in which at a certain period of the year the development may be observed. When the minute circumstances or conditions in the generation are once known, some one will undoubtedly succeed in completing that in which our knowledge of the development of the Annelides is still deficient.

Polynoë cirrata is common on the coast of Norway, and occurs between the roots of *Laminariæ*, under stones, in empty shells and other holes in which it can hide itself. It agrees perfectly, as I have convinced myself by comparison, with the Greenland species characterized by Fabricius under this name, but it never attains on our coast the immense size it does on that of Greenland.

In the months of February and March is the period of propa-

* From Wiegmann's Archiv, 1845, Part I.

gation of this Annelide: in some individuals, the body, which at other times is of a light brownish gray or whitish gray and shining with a blue reflection, is observed to have assumed a pale rose-colour. This arises from a numberless quantity of eggs which fill the common cavity of the body, with the exception of about the first anterior fourth and the feet, and appear everywhere through the skin. When the skin is cut open, the eggs are found to hang together in great masses by means of a connecting tenacious mucus. They are spherical, the yolk finely granular and opake, closely surrounded by the transparent chorion. When the egg is somewhat compressed (Plate IV. fig. 13), it exhibits the large Purkinje's vesicle without any perceptible trace of Wagner's spot. In other individuals the eggs have frequently been secreted at about the same time. They occur on the top of the back of the mother, beneath the branchiæ or so-called dorsal scales, in immense numbers, connected with one another by a tenacious mucus.

The heaps of eggs cover the whole of the hinder half of the back, but more anteriorly only the sides above the base of the feet: no eggs are met with on the seventh to the eighth front rings of the body. It seemed to me as if the eggs passed through a very small aperture just above the feet, as Rathke found to be the case in *Nereis pulsatoria*. They are all of the same size in the same individual (viz. about $\frac{1}{20}$th of a millimeter), and mostly equally developed, and therefore all of one and the same brood. Their colour is still very pale rosy red, or almost reddish white. Here, protected beneath the branchiæ, the eggs remain until the young creep out. In the meantime the yolk, between which and the chorion is a small space filled with limpid albumen, undergoes the usual process of division or furcation. Thus I once observed that the yolk had the appearance of a blackberry (fig. 14), its surface being covered with granules of different sizes, as was proved on submitting them to compression (fig. 15); each contained a bright roundish spot with a distinct outline like a nucleus, and were therefore evidently cells. On the following day, the 4th of March, the surface of the yolk had already become more finely granular, and approached again nearer to an even surface.

The ova subsequently become slightly oval, and the yolk or fœtus into which the entire yolk is converted, without any part whatever separating, is smooth, grayish white, and is more or less narrowly surrounded or inclosed by chorion (fig. 16, 17). A peculiar kind of motion was now perceptible on the separated ova under the microscope, the ova turning round and round. This was effected by the very short fringe, consisting of minute mucous filaments (fig. 16, 17 *a*), which is attached to the one extremity of the ovum, and probably covering the entire egg in the

form of a membrane, similar to the so-called *membrana nidulans* of Burdach, connects all the ova as it were by means of a tenacious mucus. This fringe is seen now and then to move slowly, and curve in a worm-like form, drawing the egg with it backwards and forwards. The cause of this motion remains a mystery to me, if it be not owing to the action of the water on the mucous substance of the fringe. The fœtus itself, which gradually acquires a bright grayish green colour, was still without motion in most of the ova; only in a few a circle of extremely minute, projecting and vibrating cilia was perceptible, which surrounds horizontally the centre of the body of the fœtus at an equal distance from the two poles of the ovum.

At last the fœtus is arrived at maturity, and the mother now carries on its back many thousands of young ones (fig. 12 *a a a*), which gradually come forth from the mucus surrounding the eggs, leave their mother and swim freely about in the water, visible to the naked eye as very minute greenish gray points ($\frac{1}{20}$th of a millimeter in size) endowed with a lively motion.

The young, which have just left the shell (fig. 18, 19), are extremely unlike the mother both in form and in structure. They are short, oval, cylindrical, unarticulated, and have, as above mentioned, horizontally round the centre of the body, a circle of tolerably long cilia (*d d*), in other respects however without any external organs. The portion of the body situated anteriorly to the ciliary circle is somewhat narrower than the hinder one, and bears two eyes (*e e*), and should therefore without doubt be considered as the head, the more so as the young one always swims with this extremity in front. The eyes are at some distance from the anterior free extremity (*b*), in the vicinity of the circle of cilia, one on each side and a little towards the back; they are very large in proportion to the body, black, and slightly elongated diagonally, or almost kidney-shaped, with the convexity turned anteriorly; not a trace of tentacula or antennæ is observable about the head.

We just now called the side where the eyes approach nearest together the dorsal side, while the opposite one, which moreover, when the young is regarded from the anterior extremity, is somewhat more projecting (fig. 19 *a*), is proved to be the ventral side, from the fact, that on it, close behind the circle of cilia, there is an aperture (fig. 18 *a*), which I look upon to be the mouth. This mouth-aperture is a diagonal fissure, whose lips are provided with vibratory cilia, which are however much smaller than those of the circle of cilia. There are also some very minute cilia at the most anterior extremity of the head (fig. 18 *b*). The intestine, as far as I could observe from the slight transparency of the body, appears

to expand considerably from the very mouth and to form a large sac, the stomach, and then gradually narrowing to proceed towards the hinder part of the body, where probably the anal aperture is situated. I could not distinctly recognise this, but I have observed it very clearly at this place in similar young of another Annelide, which will be noticed subsequently (fig. 21*f*). The colour is everywhere of a dirty pale green and only slightly transparent. The body is soft, but it rarely exhibits contractions or variations of form; it is only when the young animal is quiet, or has but little water, that contractions are perceptible on its body (and sometimes also of the intestinal canal), from its becoming broader or narrower and curving slightly at some places.

Locomotion, that is to say swimming, is effected by the vibration of the cilia. Only the large cilia of the circle effect the locomotion; the small ones near the mouth and at the front extremity of the head contribute little or nothing to it. The former correspond therefore to the powerful cilia which, in the young of the Nudibranchiæ and many other Gasteropods, effect the swimming, and are subject to the will of the animal; the latter, on the other hand, are not subject to their will, and constitute the so-called ciliary organs.

During the swimming, which is very rapid, uniform, and in all directions, the anterior portion of the head (fig. 18 *b*) is always directed forwards. Frequently these young animals revolve during swimming round their longitudinal axis: their sight is distinctly developed, for they are seen to avoid one another with adroitness, and they always swim towards the light. Although I turned the glass containing an immense number of them in various ways, they immediately swam in great troops to the side turned towards the light.

The time from the laying of the eggs till the extrusion of the young may probably amount to a couple of weeks, for I have found, in the first days of February, the cavities of the body of a *Polynoë* filled with eggs; but from the middle of this month to the middle of March, eggs on the backs in some individuals; and in others at this same period, young just on the point of quitting the backs of their mother (fig. 12 *a a*).

I kept the above-described young of *Polynoë*, which left the egg under my eyes, alive for four weeks in glasses filled with sea-water, during which time they grew it is true somewhat, but exhibited no further changes. In this respect Lovèn was more fortunate, for the young Annelides which he met with swimming freely in the sea were evidently further advanced, and therefore exhibited to him in the space of two days the further development, the tentacula, and the articulations of the body growing under

his eyes. I therefore refer to his observations, as probably the further development of our young *Polynoë* takes place in a coincident manner.

The results of the above observations are briefly as follows :—

1. *Polynoë cirrata* propagates in the months of April and March by ova which are secreted from particular apertures on the dorsal side in masses connected together by mucous filaments ; they collect on the back and under the branchiæ of the mother, where they remain during their further development and until the exit of the young. The branchiæ have here therefore a similar function as in the freshwater Mollusca (*Unio, Anadonta*), that of protecting the brood.

2. The young when they leave the egg have a very different form from that of the mother and a very imperfect structure. They are short, oval, cylindrical, unarticulated, and so to say, little more than mere head, for this occupies more than half of the entire body, and has two very distinct eyes (the full-grown animal has, as is well known, four). The mouth is a horizontal fissure on the ventral side of the body, and the anus is situated at its posterior extremity. With the exception of a circle of cilia, which surround horizontally the centre of the body and effect locomotion, there exist no other external members, no tentacula or antennæ, no feet with their appendages of cirrhi and bristles, and no branchiæ. All these organs must therefore be developed subsequently, when the true body (abdomen) has grown and become divided into articulations (as the observations of Lovèn show), as well as the two eyes, which are still deficient, while the cilia, as transitory, disappear. In short, we have here all the criteria of a metamorphosis,—different external form, parts which disappear entirely, and numerous organs which are subsequently added.

It is therefore certain that many Annelides undergo a very considerable metamorphosis. In this respect they are related to the other Articulata, and indeed most to the Myriapoda, whose young, according to the observations of Waga and Newport, leave the egg in a very imperfect state and without any articulated members.

As connected with this subject, I must mention the mucous globules which are likewise met with in the months of February and March on our coast, adhering at the depth of some feet to *Zostera marina* and *Fucus vesiculosus*. These globules (fig. 20) are about an inch in diameter, of a beautiful grass-green colour, and consist of an immense number of eggs (*b b*) enveloped in a tenacious mucus which is rolled irregularly like a riband into a knot, the whole of which is coated with a slimy envelope. The eggs are globular, filled with limpid chorion, somewhat albumen, and grass-green yolk, which I observed in all the various

forms of the process of division or furcation during its metamorphosis in the fœtus. The young (fig. 21) are, when they have escaped from the egg, short, oval, cylindrical, of a lively grass-green colour, and have the centre of the body surrounded horizontally by a circle of cilia (*d d*), while the head (*b*) is remarkable from two kidney-shaped eyes of a bright red colour, which occupy the same position as in the young *Polynoë*: these young are likewise without any articulated joints. The anus (*f*) is more distinctly visible as a small round aperture at the posterior extremity of the body than in the young *Polynoë*. They swim very quickly about in the water by means of the cilia, and always towards the light. In short, they resemble so closely the young of the *Polynoë*, that there can scarcely be a doubt of their belonging to some Annelide.

As I was unable to ascertain either the species to which these eggs and young belonged or their further development, I must content myself at present with the mere announcement, that some sea-Annelides secrete their ova enveloped in a mucous mass of a certain form, as has long been known of the leech; on the contrary, others deposit free eggs *.

EXPLANATION OF PLATE IV. FIGS. 12 TO 21.

Fig. 12. represents a *Polynoë cirrata*, natural size: a dorsal view. The yellowish gray mass, *a a a*, which covers the back (with the exception of about the anterior fourth and below and between the branchiæ), from which the young are on the point of escaping.

Fig. 13. An egg taken from the cavity of the body, magnified and somewhat compressed, to show Purkinje's vesicle.

Fig. 14. An egg taken from the back, showing the blackberry form of the yolk.

Fig. 15. The same egg very much compressed, exhibiting a bright nucleus in each of the large granules (cells) of the yolk.

Fig. 16, 17. Further developed eggs, whose yolk or fœtus is become smooth and whitish: *a* is the moveable fringe consisting of mucous filaments by which the eggs are connected.

Fig. 18. The young animal just escaped, magnified and seen from the left side: *a*, mouth; *b*, front, and *c*, posterior extremity of the body; *d d*, circle of cilia; *e*, left eye.

Fig. 19. A front view of the same animal: *a*, ventral surface; *d d*, circle of cilia; *e e*, eyes.

Fig. 20. represents the globular masses of eggs of an unknown Annelide of the natural size adhering to a piece of *Zostera marina*, *c c*: *a a*, the surrounding envelope of mucus; *b b*, the eggs.

Fig. 21. One of the young escaped from this mass of eggs: a dorsal view magnified: *b*, anterior; *c*, posterior extremity of the body; *d d*, circle of cilia; *e e*, eyes; *f*, tail.

* For instance, the *Nereides*, as I have observed in *Nereis pelagica* and in a species of the genus *Heteronereis* Oersted. I saw in the month of March an immense number of eggs, which were very minute, globular, and of a beautiful azure-blue colour, deposited one by one by both of these Annelides.